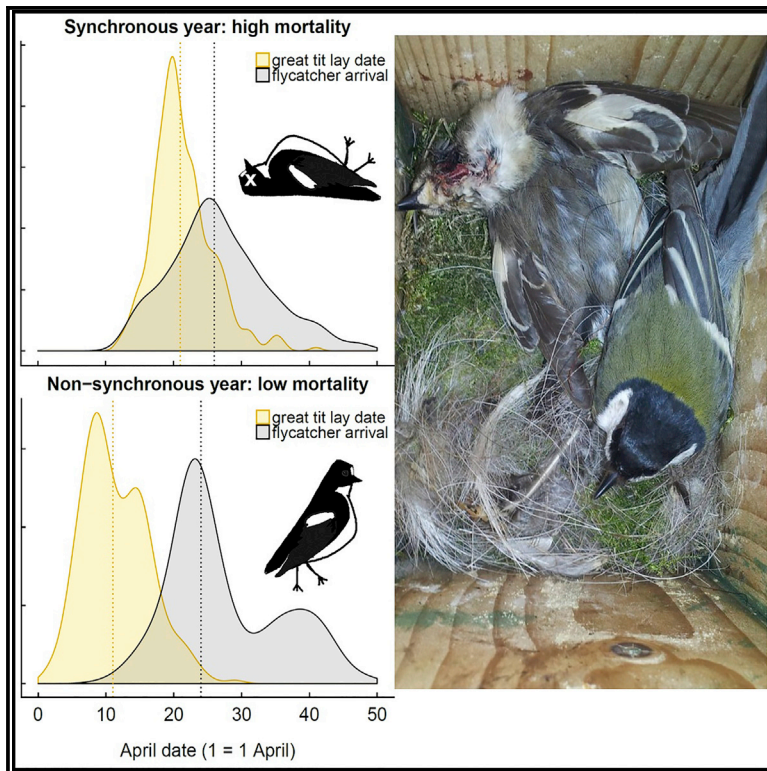


Current Biology

Climate Change May Affect Fatal Competition between Two Bird Species

Graphical Abstract



Authors

Jelmer M. Samplonius, Christiaan Both

Correspondence

jelmersamplonius@gmail.com

In Brief

Samplonius and Both analyze 10 years of breeding data focusing on pied flycatcher mortality in great tit nests. They find that resident tits and migratory flycatchers adjust to climate change at different rates and that synchrony between these species affect their fatal interactions especially in high-tit-density years.

Highlights

- Resident great tits adjust more to climate warming than migratory pied flycatchers
- Mild winters and high beech crops lead to higher nest-box occupancy by great tits
- Synchrony with tits and tit density covary with more flycatcher deaths in tit nests



Climate Change May Affect Fatal Competition between Two Bird Species

Jelmer M. Samplonius^{1,2,3,*} and Christiaan Both¹

¹Conservation Ecology Group, Groningen Institute of Evolutionary Life Sciences (GELIFES), University of Groningen, 9747 AG Groningen, the Netherlands

²Institute for Evolutionary Biology, King's Buildings, The University of Edinburgh, EH9 3JT, Edinburgh, UK

³Lead Contact

*Correspondence: jelmersamplonius@gmail.com

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SUMMARY

Climate warming has altered phenologies of many taxa [1, 2], but the extent differs vastly between [3, 4] and within trophic levels [5–7]. Differential adjustment to climate warming within trophic levels may affect coexistence of competing species, because relative phenologies alter facilitative and competitive outcomes [8, 9], but evidence for this is scant [10, 11]. Here, we report on two mechanisms through which climate change may affect fatal interactions between two sympatric passerines, the resident great tit *Parus major* and the migratory pied flycatcher *Ficedula hypoleuca*, competing for nest sites. Spring temperature more strongly affected breeding phenology of tits than flycatchers, and tits killed more flycatchers when flycatcher arrival coincided with peak laying in the tits. Ongoing climate change may diminish this fatal competition if great tit and flycatcher phenologies diverge. However, great tit density increased after warm winters, and flycatcher mortality was elevated when tit densities were higher. Consequently, flycatcher males in synchronous and high-tit-density years suffered mortality by great tits of up to 8.9%. Interestingly, we found no population consequences of fatal competition, suggesting that mortality predominantly happened among surplus males. Indeed, late-arriving males are less likely to find a partner [12], and here we show that such late arrivers are more likely to die from competition with great tits. We conclude that our breeding population is buffered against detrimental effects of competition. Nevertheless, we expect that if buffers are diminished, population consequences of interspecific competition may become apparent, especially after warm winters that are benign to resident species.

RESULTS AND DISCUSSION

Increasing spring temperatures affect the relative phenology and abundance of plants, insects, and vertebrates [2]. Within trophic

levels, competing species may show differential rates of change to temperature [5, 6], potentially affecting the strength of competitive interactions. Such interactions may be further modulated by increasing winter temperatures favoring the survival and performance of one competitor over the other [13, 14]. Density-dependent components of interspecific competition in birds have received much attention over the past decades [15], but phenological components to a much lesser extent. It is generally expected that interspecific competition intensifies when the phenological interval between two competing species decreases. Here, we show how fatal interactions between a migratory and a resident bird species are affected by climate change, because their phenologies are differentially affected by temperature and because winter warming increases the abundance of the competitively superior resident bird.

We studied pied flycatcher fatalities in great tit nest boxes in a Dutch population between 2007 and 2016. Pied flycatchers are long-distance migrants that each year travel between Western Africa and Europe [16], whereas great tits are a resident species that breed on average 16.6 days (from 7.3 to 22.9) earlier than flycatchers in our population. Fatal competition for nesting cavities with tits when flycatchers arrive has been described in previous studies [10, 17, 18], but little is known about whether climate change modulates such interactions, for example by eliciting differential phenological responses or by affecting winter survival of resident species. To test this, we scored spring arrival, a repeatable trait [19], of male and female flycatchers on a daily basis. We also collected egg-laying-initiation data of great tits and pied flycatchers in our population by doing nest-box checks every 5 days, which can be backdated as passerines normally lay one egg per day.

Competition between flycatchers and great tits for nest boxes is often fatal for the flycatcher, and we found a total of 88 flycatcher victims (86 males and 2 females) during nest-box checks, 86 of which were killed by great tits and 2 by blue tits. The dead flycatchers were all found in active tit nests and had severe head wounds, and often their brains had been eaten by the tits. Tits could exhibit a significant mortality cause on male pied flycatchers in some years, with up to 8.9% of all males (0.4%–8.9% per year) known to defend a nest box being killed in a single year, and local annual survival of males being 46% [20]. Variation among years in number killed by tits was large, and we aimed to investigate how phenology of both species and their densities affected this interaction. We performed the analyses in relation to great tit phenology and abundance.



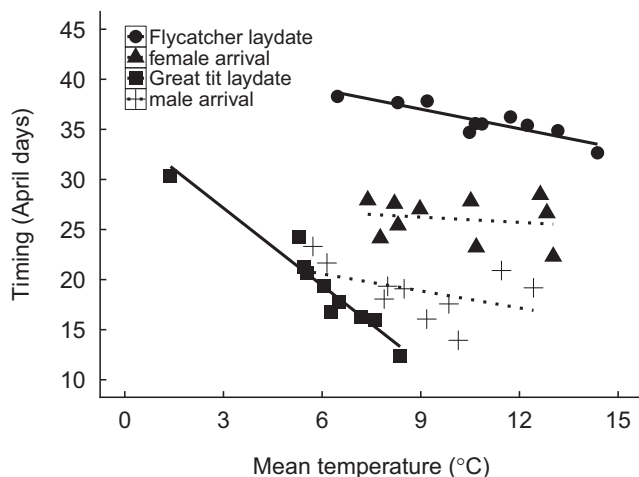


Figure 1. Differential Phenological Sensitivity to Temperature between Competing Species

Results of sliding window analysis for tit and pied flycatcher phenology in relation to local temperature. Tits adjusted mean egg laying phenology to temperature (-2.6 days/ $^{\circ}\text{C}$) significantly more than pied flycatchers (-0.7 days/ $^{\circ}\text{C}$). Flycatcher arrival was unrelated to temperature at the breeding grounds. See also [Figure S2](#) and [Table S1](#).

A total of 2,321 arrivals were scored of 1,423 individual male pied flycatchers across 10 years in ten study areas (97 area by year combinations).

We found that resident tits were more responsive in their phenology to temperature changes at the breeding grounds than migratory flycatchers ([Figure 1](#)). We analyzed this using a sliding window approach [21] to find the most explanatory climate window for annual variation in average tit egg laying, flycatcher egg laying, and flycatcher male and female arrival. Great tit laying dates responded to an earlier (February 25 to April 8) and longer (37 days) climate window than pied flycatcher laying dates (April 18 to May 2, 14 days), whereas pied flycatcher arrival dates were unrelated to temperature at the breeding grounds ([Figure 1](#); [Table S1](#)). Interestingly, the phenological sensitivity of great tit laying dates (-2.6 days $^{\circ}\text{C}^{-1}$) to temperature was about four times higher than that of flycatcher laying dates (-0.7 days $^{\circ}\text{C}^{-1}$), showing that climate change differentially affects the phenologies of these species and the interval between their breeding timing.

Climate change has enhanced winter survival of many organisms by creating milder conditions in the harshest period of the year [22–24]. We therefore expected higher breeding densities of great tits after milder winters. Using a sliding window approach [21], we found temperature in December (December 6–28) best explained annual variation in great tit nest-box occupation rates. A beech crop index ranging from 0 to 5, measured in autumn after seed fall in our study area ([Table S2](#)), was used as a covariate in the model, as this is a known predictor of great tit survival [25]. We found that the temperature in December and the beech crop index were positively correlated with great tit nest-box occupation in spring ([Figure 2](#); [Table S3](#)). Thus, climate warming positively affects the survival of the resident species, potentially increasing interspecific competition with later-arriving migrants.

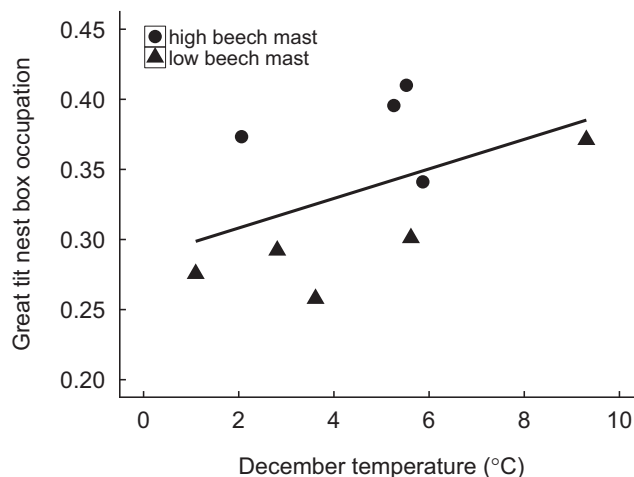


Figure 2. Great Tits Occupy More Nest Boxes after Warm Winters

Great tit yearly nest-box occupation in relation to December temperature and beech mast in the previous autumn. Great tits occupied more nest boxes after warmer winters ($p < 0.02$) and higher beech crops ($p = 0.03$, see also [Figure S2](#) and [Tables S2](#) and [S3](#)).

The annual number of flycatchers killed by great tits was clearly related to their differential phenologies and the density of great tits, and both factors were related to climatic variables ([Figure 3](#); [Table 1](#)). To test for these patterns, we ran binomial (dead or alive for each individual male flycatcher) generalized linear models (GLMs) in R 3.3.1 [26] with “synchrony between tits and flycatchers” (at the year level, as there is hardly any variation in tit-flycatcher synchrony within years among our ten study sites), “tit density” (both at the year and the plot level, as tit density varies among our study areas), and “flycatcher density” as explanatory variables among others using a model selection approach. We contrasted several covariates and used the AICc to determine the best fit model for our data ([Table S4](#)). We found that male pied flycatchers were most likely to be killed by a great tit when mean female arrival was synchronous with the population mean tit egg-laying peak, and when great tit densities were relatively high. Interestingly, the synchrony with female flycatcher arrival date was a better predictor of male mortality than male flycatcher arrival date, suggesting that competition for nesting opportunities is most intense when females arrive. Furthermore, selection operated against arriving late, as early-arriving flycatcher males were less likely to be killed than late males ([Figure 3](#); [Table 1](#)). Overall, our results suggest that interspecific competition may exhibit a substantial flycatcher mortality factor that may translate into population consequences.

To our surprise, we could not detect population consequences of fatal competition. In areas that had higher flycatcher mortality rates, we found no evidence that flycatcher population size in the following year was affected ([Figure S1](#); [Table S5](#), $p = 0.075$). This suggests that most of the mortality effects were borne by males that may not have contributed to the breeding population in the first place. Previous research showed that later-arriving territorial males had a lower probability to find a partner [12], and here we showed that such late-arriving males had a higher probability of

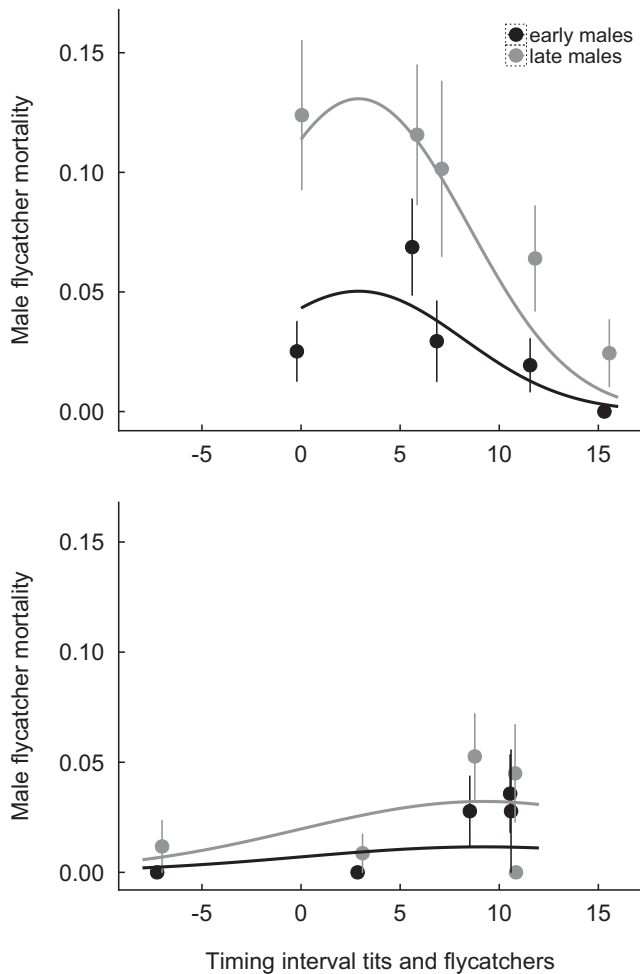


Figure 3. Synchrony with Great Tits in High-Density Years Was Associated with Higher Mortality

Probability of male pied flycatchers to be killed by a tit in relation to the interval between tit mean laying dates (LD) and flycatcher female arrival in (a) high- and (b) low-density years. The lines were fitted based on GLM outputs, where black represents relatively early flycatcher males and gray late males. See also Table 1, Figure S1, and Table S5. Error bars, SEM.

being killed by great tits. The fact that mostly late-arriving, non-breeding males were likely to be killed demonstrates that our population is to some degree buffered against the negative impacts of interspecific competition. Nevertheless, population consequences of interspecific competition may become apparent in the future if the population buffer is dwindled by this mortality.

We have shown that differential phenological responses to climatic conditions between two competing species affect a substantial mortality factor in a migratory songbird, and changes in interspecific competition within the same guild could thus be an important selection pressure on top of the more-often-reported asynchronous changes with the main food supply [27]. It is not yet clear how transferable our results are to other study systems and also whether flycatchers in the long run gain from being less synchronized with the tits or will ultimately have increased mortality because tit densities become generally

Table 1. Flycatcher Mortality by Tits in Relation to Synchrony and Tit Density

	Estimate (SE)	Z _{2312,8}	Pr(> z)
(Intercept)	−4.30 (0.460)	−9.35	<0.001
(Synchrony) ²	−0.010 (0.004)	−2.40	0.016
Synchrony	0.109 (0.056)	1.96	0.050
Year tit density	18.54 (4.42)	4.20	<0.001
Plot tit density	4.85 (1.22)	3.98	<0.001
Local flycatchers	−0.615 (0.269)	−2.29	0.022
Late flycatcher males	1.04 (0.236)	4.42	<0.001
Flycatcher density	0.874 (0.971)	0.90	0.368
(Female arrival) ² × year tit density	−0.129 (0.052)	−2.46	0.014

“Synchrony” refers to the difference in timing between great tit mean laying date and flycatcher female arrival date. Local flycatchers refer to birds ringed in our population. Late flycatchers were defined as the latter 50% of arriving males in relation to the year mean. All predictor variables were centered by subtracting the mean. See also Figure 3.

higher due to milder winters. The severity of each of these processes (i.e., tit density and tit-flycatcher synchrony) would also depend on the extent to which winter and spring warming fluctuate independently. An analysis of the correlation between average winter (December and January) and spring (April and May) temperature between 1901 and 2016 suggests that the two processes can fluctuate relatively independently, as winter temperature only explains a small proportion of variation in spring temperature ($R^2_{\text{adj}} = 0.064$, Figure S2). Future experimental work could focus on manipulating tit and flycatcher timing and densities.

Resident species have been shown adjusting to temperature through phenotypic plasticity [28], but migratory species are apparently not as responsive to temperature changes [6, 7] and may require an evolutionary response for adjusting to climate change. These differential responses may in general affect the competitive interactions between residents and migrants, with migrants likely suffering from stronger interspecific competition due to increased resident densities and breeding at a less favorable time in relation to the caterpillar peak. On a larger biogeographic scale, higher-latitude breeding sites that harbor a relatively large fraction of migrants [29] may change in community as residents increasingly survive the milder winters and outcompete migrants that adjust more slowly to ongoing advancements of spring. Predicting the future responses of communities to ongoing climate change thus requires not just the knowledge of how different species respond relative to the phenology of their food but also how their interspecific competitive interactions will be changing.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures and five tables and can be found with this article online at <https://doi.org/10.1016/j.cub.2018.11.063>.

A video abstract is available at <https://doi.org/10.1016/j.cub.2018.11.063#mmc3>.

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AUTHOR CONTRIBUTIONS

The study was designed by J.M.S. and C.B. Field work was performed by J.M.S. and C.B. Analyses were done by J.M.S. The manuscript was written by J.M.S. and C.B.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
<i>Ficedula hypoleuca</i>	Nest box study, Groningen	Christiaan Both
<i>Parus major</i>	Nest box study, Groningen	Christiaan Both
Deposited data		
Data accessible	DataverseNL	https://hdl.handle.net/10411/CLFZBQ
Software and Algorithms		
R (Rstudio)	The R foundation	https://www.r-project.org/ ; https://www.rstudio.com/

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed and will be fulfilled by the Lead Contact, Jelmer Samplonius (jelmersamplonius@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study species and area

This study was conducted in National Park Dwingelderveld (52°49'5"N, 6°25'41"E) and Drents-Friese Wold (52°52'48"N 6°18'36"E) in the Netherlands across ten study plots with 950 nest boxes in total (dimensions W x D x H: 9 x 12 x 23 cm) between 2007 and 2016. Mean first egg date phenology differed between the main occupants of the nest boxes great tits averaging 19.3 April ($n \approx 300$), and pied flycatchers 5.9 May ($n \approx 280$). Pied flycatchers are long distance migrants that travel each year between Western Africa and Europe [16], whereas great tits are residents. There was substantial annual variation in the interval between great tit and flycatcher first egg date phenology, which fluctuated at the extremes between 7.3 days in 2013 and 22.9 days in 2014. Ethical supervision of the project was provided by personal permits from the Dutch Flora and Fauna law and ringing licenses by the Vogeltrekstation.

METHOD DETAILS

Arrival scoring

During the breeding season, plot checks were performed usually at five day intervals starting in late March until the end of June. Standard population metrics including first egg date, clutch size, and hatch date were determined for all nest box breeding species. Pied flycatcher parents were also caught, ringed, and measured (weight, tarsus, wing length) and the nestlings were ringed and weighed at day 7 and 12 after hatching. Pied flycatcher arrival, a repeatable trait in our population [19], was scored every other day at the minimum, but often daily. It was done in a standardized way by recording location and individual variation in plumage characteristics, augmented by ringing information. All individuals were later caught when they were breeding. Details on our arrival scoring methodology are published elsewhere [19]. In total, we scored 2321 arrivals of 1423 individual males, and 2008 arrivals of 1491 females across 10 study areas in 10 years with 97 area by year combinations (three areas had no arrival data in the first year of the study).

Victim identification

Pied flycatcher victims were collected during regular plot checks, and were usually directly visible on opening the nest box. Date of death was determined as the average between the last known sighting of the male and the date it was found. Sometimes flycatcher males were interweaved within the nesting material and were only discovered later, after which we determined the last day that the individual had been recorded singing and determined date of death as the average between the last known date of being alive and the date of the nest box check in which it was not seen.

Beech mast data

Beech mast data was collected every year by a local field ecologist, Rob Bijlsma in one by one meter transects ($n = 30$ beech trees), using an index system between zero and five. An average number of beech nuts was computed by taking the average number of beech nuts per square meter, and computing a score out of that (Table S2).

QUANTIFICATION AND STATISTICAL ANALYSIS

Sliding window analysis

To determine the phenological sensitivity of great tits and pied flycatchers to temperature, we used a sliding windows approach with the *climwin* [21] package in R 3.3.1 [26]. Temperature data from the nearby (15–30km) weather station Hoogeveen (52°45'00"N, 6°34'12"E) was freely available from the Royal Dutch Meteorological Institute (KNMI). Reference dates used for the sliding window were the mean phenology of great tit (20 April) and pied flycatcher (6 May) egg laying date and pied flycatcher female arrival (26 April), rounded up to the next integer, using temperature windows of up to 60 days before the reference date for egg laying, and up to 30 days for female arrival. For great tit occupation rates we used 1 March as a reference date, and included "beech mast index" in the sliding window analysis, using windows of up to 120 days before 1 March, and excluding temperature windows shorter than two weeks.

Model selection parameters

To study phenological and density dependent components of flycatcher mortality by tits, we implemented binomial GLMs in a model selection approach using the R package *AICcmodavg* [30], with flycatcher "alive/dead (1/0)" as a response variable, and contrasting the linear and quadratic terms "Sync male" (the mean male flycatcher arrival date subtracted from the mean tit egg laying date), and "Sync female" (the mean female flycatcher arrival date subtracted from the mean tit egg laying date), and including or excluding the linear terms "year tit density," "plot tit density," "early/late males," and "Immigrant / Local" (Table S4). We also included an interaction term between "year tit density" and "Synchrony," as we expected that the quadratic effect could increase in high tit density years. *A posteriori* we also included "flycatcher density" in the best model (model 15, Table S4) to establish whether flycatcher density could explain part of the variation in the likelihood of mortality.

Justification of parameters

The reason we contrasted male and female arrival date was, because we expected that males might be more likely to engage in risky behavior when females started arriving (which we found to be true). Quadratic terms were included, because we especially expected competition to be intense during great tit egg laying [10, 17], so if flycatchers arrived before or after that, there would be less mortality. All our densities were calculated as nest box occupation, since our nest boxes are spaced equally (about 30 m apart). Therefore, density parameters theoretically could vary between zero (no boxes occupied) and one (all boxes occupied). The categories "Early" and "Late" males were established by assigning them to either the first 50% of males that arrived, or to the latter 50%, based on their arrival date. We expected that later males would suffer more mortality, because they may engage more in taking over a high quality site from a tit as a result of them being less likely to get a partner [12]. The categories "Immigrant / Local" were assigned to birds that had been ringed in or recruited to the population (local) and to birds that had never been seen there before (immigrant). This parameter was included, as we expected local birds to be more familiar with the area and to avoid great tits relatively more.

Model selection analysis

To establish the right level of analysis, we first considered the year scale, and then zoomed in on the plot level scale, using a two-step approach (Table S4, models 1–8 are at the year scale, models 9–15 also include the plot level scale). We used AICc scores to determine the best model. We considered the best model to be the one with the lowest AICc by at least 2 AIC points compared to the second best model. There was so little variation in tit egg laying dates and flycatcher arrival dates among our study areas that we considered it pseudo replication to analyze "synchrony" at the plot level. There was however substantial variation in tit densities at the plot level, so to establish any residual variance not explained by year level densities, we subtracted plot level densities from year level densities to get an estimate of the residual tit density at the plot level (plot tit density). Other covariates were irrelevant to consider at either the year or the plot level. A detailed overview of parameters included and excluded can be found in Table S4.

Population effects

To study whether tit induced mortality exhibited any negative consequences on flycatcher population growth, we calculated for each plot and year the percentage of males that was killed. We then calculated the population growth of flycatchers within that plot for the following by dividing N_{t+1} by N_t . The year 2007 was excluded, because the population was established in that year and we wanted to exclude the effect of a growing population. The slope of population growth over mortality was calculated using a linear mixed effects model (LMM) where population growth was the response variable, and "mortality percentage" was used as a predictor variable. "Year" and "site" were used as crossed random intercepts (Figure S1, Table S5).

DATA AND SOFTWARE AVAILABILITY

The accession number for the data reported in this paper is DataverseNL: <https://hdl.handle.net/10411/CLFZBQ>